GLASGOW

# Relations & Distribution of Phyllophaga Harris (Lachnosterna Hope) in Temperate North America

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# RELATIONS AND DISTRIBUTION OF PHYLLOPHAGA HARRIS (LACHNOSTERNA HOPE) IN TEMPERATE NORTH AMERICA

BY

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY

Robert Douglass Glasgow

ENTITLED On the Evolution and Dispersal of the Genus Phylloph-aga Haris (=Lachnosterna Hope.)

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE

DEGREE OF Doctor of Philosophy

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In Charge of Major Work

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# INTRODUCTION

In beginning the studies reported in the following paper, it was the original purpose of the writer to take up first, the geographical, ecological, and phylogenetic relations of the species of Phyllophaga which occur in temperate North America, and to extend the work later, as opportunities arose, to include the species of other regions. Very early in the course of the work however, it became evident that the best arrangement of the genus that had been published - that of Dr. Horn - did not represent well the natural relationships of the groups and species, and that most of the collections and published lists of the genus were in such a chaotic condition with regard to accuracy of determination, that the available, dependable data were wholly insufficient to permit the proposed series of studies to be started at the point indicated.

It became necessary therefore, as a preliminary to the accomplishment of the primary object of this work, to begin at the bottom, and to revise the group from the beginning; and since, as will be shown later, the forms in many cases can be certainly distinguished only by reference to the genital characters, it was determined that this revision should be based upon the dissection and direct examination

of the genital characters of the actual type specimens, as far as this might be possible.

These preparations for the revision of the group were accompanied by the accumulation of quantities of material and data, as completely representative of this group as possible; and since it was evident that several of the groups of the genus occurring within the territory to be studied, had been derived independently from different, outside centers of origin, the studies were extended to include the possible sources from which these forms probably penetrated the regions that they now occupy.

This difficult and time consuming process has now reached a point where a knowledge of the genital characters for all of the type specimens of the species of temperate North America that, so far as can be determined, have escaped destruction, a knowledge obtained by personally dissecting out and studying these organs from the type specimens in the American Museums, and from drawings prepared for this work from the genital organs dissected from the type specimens in the European Museums, together with a general study of the geographic relations of the various forms, has made it possible to clear up, it is hoped completely, the taxonomic confusion that to a greater or less degree has characterized all of the preceding work

on this genus.

Sufficient data have also been accumulated to warrant the following conclusions regarding the probable origin and relationships for the various groups of the genus represented in temperate North America.

These studies were carried on under the supervision of Professor S. A. Forbes, who has followed the work with keen interest, and who has always been ready to give freely, for the purpose of extending advice or pertinent suggestions regarding the solution of some difficulty, time that was already too fully claimed by other duties.

The writer is greatly indebted to Professor Forbes for the use of data belonging to the State Entomologist's Office, and for the use of the enormous collections of Illinois species of Phyllophaga aggregating over 100,000 specimens, which belong to the Illinois State Laboratory of Natural History; and it should be stated here that the results already obtained would have been wholly impossible, but for the encouragement and cordial assistance constantly given toward the work by Professor Forbes, and the persistent exertion of his influence among entomologists toward securing for the writer the unusual privilege of dissecting the type specimens in the American Museums, and in arranging for having such dissections made of the types in the European Museums.

The writer wishes also to acknowledge his great obligation to Dr. C. C. Adams for many invaluable suggestions regarding the faunal relations of the various regions of North America, for many valuable references to the literature of the subject, and for the use of numerous papers that were readily accessible only in his private library.

## STATUS OF THE NAME PHYLLOPHAGA

The name Phyllophaga Harris is used in this paper instead of Lachnosterna Hope, for the reasons indicated below.

Hope proposed the name Lachnosterna in 1837 (Coleopterist's Manual, Vol. I, p. 99), and this name, having been adopted by LeConte, and following him, by Horn and by Smith, came to be accepted by American entomologists.

This name, however, is antedated by Dejean's name Ancylonycha, published in the catalogue of his collections in 1833, and Dejean's name has been accepted by Erichson, Lacordaire, Burmeister, and all of the leading entomologists of Europe.

Both of these names, however, were anticipated by Dr. T. W. Harris, who in an essay upon the "Natural History of the Rose bug", published in Massachusetts Agricultural Journal and Repository, Vol. X, No. 1, July 1826, makes the following note on page 6:

"The genus Melolontha as constituted by Fabricius contains a vast number of species, differing greatly in external appearance, and somewhat in modes of life. Fabricius describes 149 species, and Schönherr, after separating those which constitute the modern genera Anisonyx, Glaphyrus, Amphicoma, Rutela, and Hoplia, enumerates 226 species of

Melolontha, to which additions are constantly making from the discovery of new species. Hence the genus requires further subdivision. The bases of these subgenera have been pointed out by Latreille, Knoch, and Schönherr, and some have already been established. I would restrict the name of Melolontha to those species which have more than three lamellae to the club of the antennae, like the vulgaris of Europe, and of which we have an indigenous example in the M. decimlineata, of Say, (M. occidentalis Herbst?). Our common species quercina, hirsuta, hirticula, balia, and some others might receive the generic name Phyllophaga. M. vespertina sericea and iricolor would form another subgenus might be called Stilbolemma, unless they are included in Serica MacLeay, or Omaloplia of Megerle; the characters of their genera I have not seen. M. pilosicollis, longitarsa, and moesta of Knoch and Say should each constitute a subgenus. The latter (with M. sordida and frondicola Say?) belongs to Kirby's genus Apogonia. From the singular manner in which the nails are divided at tip, I would call the linearus of Schönherr Dichelonyx."

It seems, therefore, that no choice remains but to accept the name Phyllophaga for the genus of which "quercina, hirsuta, hirticula, and balia" form a part; and no type having previously been assigned for this genus, hirticula, one of the four species originally included by the author of the

name, and at the same time one of the most strongly marked, one of the most widely distributed, and probably the most abundant species in the group, is proposed as the one best qualified to represent it. Figures prepared from Knoch's type specimen are given in Plate

Since a readjustment is necessary to bring the American and the European entomologists into harmony regarding the name of this genus, and since the Americans, who are naturally most concerned with the group because of its economic importance in the United States, are practically the only ones except systematists who would be affected, it is not likely that even the most enthusiastic advocate of an arbitrary fixity of nomenclature would object to the adoption of the earliest proposed name in the course of that readjustment.

## STATUS OF THE GENUS PHYLLOPHAGA

Probably no group of terrestrial animals offers more promising material than does the Scarabaeid genus Phyllophaga Harris (=Lachnosterna Hope), for study as an index to certain phases of faunal development, or as a means of throwing light on some of the problems concerning the factors which have to do with the modification or evolution of biological forms, commonly termed the origin of species.

This genus is relatively ancient, it has an extended range, and it contains a large number of closely related species, many of which are widely distributed and highly variable; and while the species for the most part are of large size and abundant wherever they occur, they are notably sedentary (nonmigratory) in their habits. The genus is also of great economic importance; but in spite of its many claims upon the attention of students, few genera containing species of moderate size have been so much neglected.

The reason for this neglect is obvious, however, for first, in many of the groups of this genus, the forms are notoriously difficult to separate except upon internal genital characters, the use of which requires a partial dissection of the specimen in mounting; second, the original descriptions are nearly all based exclusively on superficial characters, and often are wholly inadequate for the recogni-

tion of the species; and third, the type specimens are very widely scattered, many of the types being in various European Museums; and those of all the earlier workers being mounted without having the genitalia extruded, they were wholly inaccessible, or inaccessible for effective comparison, up to the time that the present series of studies was begun.

The difficulties encountered when the genus is studied without the aid of the special genital characters mentioned above, may best be understood from a statement by Dr. George H. Horn*, than whom no entomologist has ever done more painstaking, or more valuable work on the genus.

"It is not surprising that attention has not been given to the species of Lachnosterna, as the literature at present available does not give great assistance, and in my own case there was almost equal difficulty in arriving at a correct determination of the species with the types for comparison along with the literature."

"Lachnosterna is certainly one of the most difficult genera in our fauna ---- ."

The work of the two great coleopterists, LeConte** and

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* Horn, Geo. H., M. D., "Notes on Lachnosterna.", Entomologica Americana, Vol. III, p. 141.

** LeConte, John L., M. D., "Synopsis of the Melolonthidae of the United States.", Jour. Acad. Nat. Sci. Phila., Series II, Vol. III, pp. 225-288, 1856).

Horn*, who successively revised this genus, while based exclusively on superficial characters, was wonderfully successful and accurate in view of the difficulties presented by the problem; and it is only restating these difficulties in stronger terms, and in no way a reflection upon the quality of their work to say that their determinations, based upon the totally inadequate descriptions of the earlier workers, were often incorrect, and that both authors themselves sometimes described composite species on the one hand, or described the same form under several different names on the other hand.

Since the publication of Horn's "Revision", the only important contribution to the study of Phyllophaga is the work of John B. Smith**, "Notes on the Species of Lachnosterna of Temperate North America".

In this paper, Smith figures the genitalia of nearly all of the species then known, but in his work he does not

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* Horn, Geo. H., M. D., "Revision of the Species of Lachnosterna of North America North of Mexico.", Trans. Amer. Ent. Soc., Vol. 14, pp. 209-296, 1887.

** Smith, John B., "Notes on the Species of Lachnosterna of Temperate North America.", Proc. U. S. Nat. Mus., Vol. II, pp. 481-525, 1888.

attempt to modify Horn's arrangement of the group in any way, although he points out several of the more obvious inconsistencies which only a reference to the genital characters could show. From the nature of his work, which he states was not intended as a contribution to systematic entomology, but rather to be supplementary to the revision of the genus published by Dr. Horn, Smith made no effort to clear up the numerous errors that, owing to the inadequacy of the superficial characters alone, had unavoidably crept into Horn's work; but the series of figures of the genital characters published by him, although sometimes a little crude, excepting only the work of Dr. Horn, was undoubtedly the most valuable contribution to the study of the genus that had yet been made.

# TAXONOMIC VALUE OF THE GENITAL CHARACTERS IN COLEOPTERA

About the middle of the last century, European authors had begun to recognize the importance of the characters presented by the genital organs of beetles, for the recognition of species, and in a paper on this subject published in 1882, Kraatz* figures the male genitalia of three North American species of Phyllophaga. Regarding the taxonomic significance of these structures Kraatz** says in another article:

"1. Grössere, natürliche Gruppen zeigen line typische Form des Penis, jedoch nicht immer."

"2. Die Natürlichkeit einzelnen Gattungen kann durch die abweichende Gestalt des Penis bei dem Mangel auffallender Äusser Merkmale gleichsam im Wege der Ergäuzung nachgewiesen werden."

"3. Die meisten arten, und bisweilen gerade sehr ähnliche, zeigen eine, oft merkwürdig verschiedene Penis-Bildung."

The male genital characters have been used with advantage repeatedly in the study of various groups of Coleoptera, but they have been found also to be valueless for specific distinction in some genera.

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* Kraatz, Dr. G., Deutsche Ent. Zeit., Vol. 26, pp.123-124, pl. 3, figures 33, 34, and 36, 1882.

** Deutsche Ent. Zeit., Vol. XXV, p 116, 1881.

The most comprehensive work on this subject is the recently published Memoir of Sharp and Muir*, entitled "Comparative Anatomy of the Male Genital Tubes in Coleoptera." These authors assign great taxonomic value to the male genital structures, and base upon them a very interesting series of conclusions regarding the probable phylogenetic relations within the order.

Regarding the manner in which Smith came to study the genital characters of Phyllophaga, that author says:

"In the course of our collections I first noted in specimens taken in coitu a difference in the appearance of the male genitalia. I am aware that in a somewhat fragmentary way the genitalia of some genera of Coleoptera have been studied in Europe, and that a few of our Scarabaeidae had also been studied in connection with European species, but I have made no exhaustive study of the literature of this subject. In this country Dr. Horn has made use of the sexual structures in his study of the species of Corphyra, but, so far as I am aware, no other American author has made anything like a systematic attempt at their study."

"The positive results seen by me in my studies of these organs in the Lepidoptera, led me to a careful examination of them in the species here, in the hope that here might be the character by which the species of the fusca group could be

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* Trans. Ent. Soc. Lond., 1912, Pt. 3, pp. 477-642, 37 plates.

finally and satisfactorily separated. The hope was realized even more fully than I had expected, and the great differences found in the males led to an examination of the females for correlated structures which proved as distinctive as those of the male, and which so far as I am aware, have not been hitherto studied", (Notes on Lachnosterna, p. 480).

In the genus Phyllophaga the genital structures are usually characteristic of the species to a remarkable degree; a fact that is extremely fortunate in a group, the species of which are so difficult to separate by superficial characters alone. Indeed, forms in some of the groups that are practically indistinguishable superficially, can be distinguished at a glance when these characters are referred to.

These characters, however, are not so characteristic in all of the groups of the genus, and occasionally their value in comparison with other characters will scarcely justify the trouble of extruding them in mounting the specimens.

# GEOGRAPHIC DISTRIBUTION AS AN INDEX TO THE PHYLOGENY OF INSECT GROUPS

It has been suggested that insects in general do not afford promising material for studies upon which to base conclusions regarding the origin and the course of development of present faunal relations. (Ortmann, Distribution of Decapods and Ancient Geography). Ortmann bases his opinion upon the fact that "the majority of insects possess unusual means of dispersal (power of flight) that are apt to obscure the original conditions of distribution". If this were true, studies of the geographic relations of an insect group would promise little information bearing on the probable phylogeny of the group.

That the possession of wings introduces a factor which is likely to " obscure the original conditions of distribution", is however, by no means generally true of insects. On the contrary, many insects that have highly developed wings are notoriously sedentary in their habits. For example, the reappearance of the seventeen year and the thirteen year Cicadas in the same places has been observed and recorded, generation after generation, in some instances for over two hundred years; and regarding the characteristic irregularity of local distribution within the immediate region occupied by a single year's brood, Marlatt says (Bull. 71,

Bur. Ent., U. S. Dept. Agr., p. 101): "The local abundance of the Cicada in well-defined districts is to be explained by the fact, already noted, that the winged insect is sluggish, and scatters but little from the point of emergence, which, with favoring circumstances, tends constantly to concentrate rather than to scatter the species."

The European May beetle, Melolontha vulgaris, also affords an example of the non-migratory habits of an insect which possesses in a high degree, the "unusual means of dispersal" mentioned by Ortmann. This beetle is the only common species of the genus in large parts of France and Germany, it has a three year life cycle throughout much of its range, and like the Cicadas mentioned above, tends to occur in definite broods, appearing in great numbers only once in three years. This insect is enormously destructive, sometimes becoming almost a veritable plague during its years of greatest abundance, - the so-called "Flugjahre" or Maikäferjahre, and because of its great economic importance it has been very closely studied and observed. Records show, as indicated above, that the broods of different years are not generally distributed; but rather, that they are broken up, and occur separately in isolated districts, so that three contiguous districts may each have its own series of Maikäferjahre which alternate triennially with those of the other two. The persistence of these different Maikäfer

flugjahre in immediately adjoining districts has been observed for long series of generations, and has occasioned a great deal of comment.

Habitual or erratic migratory movements are relatively rare among insects, and the great extensions that are known recently to have been made in the range of certain species, such as the Colorado potato beetle, Leptinotarsa 10-lineata, the cotton boll-weevil, Anthononomus grandis, and the box elder bug, Leptocoris trivittatus, have been induced or accelerated to a greater or less degree, it is true, by the influence of man; but nevertheless, these movements have been just as spontaneous a response to environmental conditions as any so-called normal insect movement, they have been governed as rigidly by the same fundamental, biological laws that have controlled the dispersal of animals since the most remote past, and they present many of the same general phenomena that have characterized those insect migrations in the past which have contributed so largely to determine the character of our present insect fauna.

While the wings of a few of the species of Phyllophaga are either wanting or functionless, by far the greater number of the species are rather strong fliers; but the pronounced tendency toward a concentration of the grubs in the vicinity of the food plants frequented by the adults, and the striking difference in relative dominance of different members of the same series of species in little separated and very similar situations, show that extensive movements of the beetles

probably do not occur.

On the whole, it appears that the possession of the power of flight in itself does not necessarily render insects less valuable than other groups of animals as a medium through which to study the conditions of animal distribution.

## CHARACTERS OF THE MALE GENITAL TUBE IN PHYLLOPHAGA.

The terms applied by Sharp and Muir to the various parts of the typical Coleopterous male genital tube (see explanation of terms), have been adopted in this paper for the corresponding structures that are treated here.

As in Coleoptera in general, the complete male genital tube in Phyllophaga consists properly of two portions; the seminal ducts leading from the testes form what is termed the zygotic portion by Sharp and Muir*, and the remaining long, single, highly irregular tube, turned back over itself and joined to the body wall forms what is termed the azygotic portion or the azygos by the authors named above. The paired or zygotic portion with certain related glands is held by Escherich** to have been derived from the mesoderm, while the remaining, azygotic portion, with its accessory glands is held by the same author to be of ectodermal origin. In the present series of studies we are concerned only with the unpaired azygotic portion of the tube.

The male genital tube in Phyllophaga is relatively simple. The basal piece is strongly developed, and the lateral lobes are typically united above to form a yoke-like structure something like an inverted U. The lower points of this U-shaped structure may or may not be united by a chitinous bridge which, when present completes a ring-like or collar-like structure through the opening of which, the internal sac is

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*Sharp & Muir. Trans. Ent. Soc. Lond. 1912,part 3,pp.477-642

**Escherich. Zeitschs. f.wiss. Zool. Vol.57,1903,p.620.

evaginated. Usually the median lobe is absent in the species of temperate North America, but in the tropical species, this portion of the tube is highly developed, and presents extremely valuable characters for the recognition of the species. In the species of temperate North America, in which the median lobe is absent, the lateral lobes are usually modified in such a manner as to afford ample means for separating the species, even in the more generalized forms.

## GENETIC RELATIONS OF THE GROUPS OF PHYLLOPHAGA WHICH OCCUR IN TEMPERATE NORTH AMERICA

In arriving at the conclusions here presented regarding the probable phylogenetic relations of the subdivisions of the genus Phyllophaga that occur in temperate North America, the evidence secured from a critical study of the male genital characters and of such other dependable characters as the forms have been found to present, was correlated with the evidence produced by an analysis of the geographic distribution of the various groups, and of their geographic and structural relations with the allied groups of tropical America, as far as the available extra- limital material made it possible to do this.

The forms occurring in Temperate North America which have been assigned to the genus Phyllophaga, seem to fall naturally into at least four series of more or less clearly defined groups.

These series and groups are based upon the male genital characters rather than upon the primary superficial characters used by Horn in his arrangement of the genus, and the characters used by Horn, when given what seems to be more nearly their normal value, supplement very consistently the arrangement based primarily on genital characters.

In speaking of the difficulties in classification presented by the remarkably homogeneous character of this assemblage of species, Horn says: "The only possible division of the genus on characters at all constant would be indicated by the sexual characters of the hind tibial spurs of the male, -----."

In the genus Phyllophaga, the hind tibiae are provided apically with two spurs, situated on the sub-truncate end of the tibia near its junction with the first tarsal segment. In the females, both of these hind tibial spurs are articulated with the tibia and are freely movable; but in the males there may be two movable spurs, or only one, and where the male hind tibia bears only one movable spur, the inner angle at the distal end of the tibia is usually produced into a spur-like process -- the so-called fixed spur of Horn, and of LeConte.

Of the character just described, Horn says: "We owe to Dr. LeConte the observation that two primary series exist in Lachnosterna; first, those in which the posterior tibial spurs of the male are both free and movable; second, those in which the inner spur is fixed, while the outer alone is movable." And farther on he says: "-----in some of the males of the second series above indicated, the fixed spur may be very short or entirely absent, as in prununculina, etc."

When applied to the forms occurring in temperature North America, the character afforded by the male hind tibial spurs offers a convenient and readily used means of dividing the genus into two clearly defined sections, neither of which, however, is a homogeneous or continuously related series of species, and the use of this character would separate many closely related forms, if both

the Antillean and the continental species of the genus are considered together.

In preparing his table of species for this genus, Horn took the structure of the male hind tibial spurs as a character of first importance, giving for his reason, "as there is here no variation." Horn relied too implicitly on this belief, however, and as a result of the variability of the fixed spur, redescribed a short spurred specimen of crassissima Bl. as a member of the ephilida group, under the name generosa.

Apparently the fixed spur has not resulted from an anchylosis of the joint and the coalescence of the base of the inner free spur with the tibia. On the contrary it seems more probable that one of the free spurs was lost in those forms possessing a fixed spur, and that, in the great majority of such cases, the adjacent angle at the distal end has developed into a spur-like process.

That such is the case, and that the course of evolution has not run in the opposite direction, is indicated by the following evidence.

The presence in this genus of two movable spurs on the male hind tibia indicates a more generalized condition than that characterized by the presence of one movable and one fixed spur; that is, the presence of a fixed spur is evidence of specialization, because:

1. The presence of two free spurs is a characteristic, not only of this genus, but also of the genera of all but one of the tribes of this division of the sub-family Melolonthinae

Both hind tibial spurs free, is therefore an ancestral character.

2. The fixed hind tibial spur rarely occurs in those forms which are characterized by the more primitive types of genital structures; and it does occur quite uniformly in those forms which are characterized by the more highly specialized types of genital structures.

Therefore the forms in this genus which have one of the hind tibial spurs fixed, evidently appeared later than, and were derived from, forms which had both hind tibial spurs free; and this character affords a criterion which may be used as an index to the direction of the movement along the lines of dispersal, in determining the probable centers of origin for the various groups.

## THE PRIMARY DIVISIONS OF PHYLLOPHAGA IN TEMPERATE NORTH AMERICA

1. The fusca-rugosa series:

This is the dominant series of temperate North America, it is confined to that region, it is sharply differentiated from the other two series with which it is associated, and apparently its nearest relatives occur in South America.

2. The congrua-dispar series:

In temperate North America this series is typically an element of the southeastern and southern coastal plains fauna, and structurally, the forms composing it are very closely allied to the Antillean section of the genus.

3. The crenulata series:

Typically southern and southwestern in temperate North America, this series reaches its highest development in the southwestern United States and Mexico. It continues through Central America into South America, and while it is related to certain elements of the Antillean section of Phyllophaga, the relationship is apparently more remote than that of the preceding series.

4. The tristis series:

This series is represented outside of the southwestern part of the region under consideration only by the single species tristis Fabr., but this species is common throughout the

greater part of the eastern United States. It appears to be more typically Mexican and Central American, and it extends also into South America.

Its relationship to the other series outlined in this paper is obscure, and can be determined clearly only by a greater knowledge of the forms occurring in Mexico and Central America than it is possible to secure from the limited amount of material that is now available. Apparently this series has no near relatives in the Greater Antilles.

## THE FUSCA RUGOSA SERIES

The dominant series for temperate North America, and the only one of the four series occurring there whose range is confined to that region, this section of the genus Phyllophaga, more than all the rest, presents a subject of commanding interest to students of the fauna of eastern North America.

Sharply separated from the other series of the genus with which it is associated, and distantly isolated from its nearest relatives, which occur in South America, and which, on their part, are not very much more nearly related to the other sections of Phyllophaga, the fusca-rugosa series is a characteristic, indigenous element of our fauna, in comparison with which the other series are relatively recent additions.

This series is characterized throughout by the fact that the tegmen consists of an approximately symmetrical, basal, collar-like portion, articulated proximally on each side with the basal piece, and produced apically into two usually strongly asymmetrical lateral lobes, which may be sculptured or modeled into a seemingly endless variety of forms. The characters presented by the male genital tube, are very strongly marked, and give little suggestion of any probable immediate relationship with the other series represented in the region studied. The species rugosa Melsh, hornii Smith, hirticula Knoch, infidelis Horn, fervida Fabr., and drakii Kirby, are representative, strongly marked forms of the series.

The problem of determining the probable relationships and the probable ancestry of the series was peculiarly difficult.

Clearly it was not at all closely related with any of the associated series of temperate North America, and the only course remaining was to make a systematic examination of the genital characters of material in the genus foreign to the region under consideration, for some clue pointing toward a possible source from which it might have come.

This series is unique among the Phyllophaga of the entire western hemisphere, as far as the available material shows, in the fact that the arch formed by the united lateral lobes of the male genital tube, as previously stated, has a more or less symmetrical, collar-like base, upon which the two asymmetrical lateral lobes are superposed. Therefore, as a plausible working hypothesis, it was taken to be possible that the basal collar represented the original, symmetrical pair of lateral lobes characteristic of the primitive type of male genital tubes in Scarabaeidae, and that the symmetrical, apical lobes of the arch were developed through the fusion with the primitive symmetrical tegmen, of a type of median lobe which bore a pair of asymmetrical lobes at its apex. A median lobe of this type occurs in other groups of Coleoptera, and a diligent search was accordingly begun, to discover whether a generalized type of this kind could be found among the more promitive species of the genus.

The Mexican forms studied presented nothing suggestive, and while the male genital tube in the Antillean species often has a highly complex and strongly asymmetrical median lobe, the form of this median lobe is of such a nature that it could not possibly be made to conform to the hypothesis.

Finally, however, a few specimens were found in some material from the Lesser Antilles, which gave the key to the problem. This material contained two very similar forms, one from Trinidad, and the other from St. Vincent Island. The form from St. Vincent Island was representdd by a male and two females, fortunately pinned without having had the genitalia exposed. It is said fortunately "because it seems not to be generally known among entomologists, that in many beetles and particularly in the tropical species of Phyllophaga, the median lobe of the male genital tube bears practically all of the distinguishing characters, and in mounting material with the genital structures exposed, many specimens are ruined for critical study, by having the median lobe of the male tube broken off and thrown away.

The genital tube of this male specimen from St. Vincent Island (Plate XII ) proved to be exactly the type required by the hypothesis stated above, for explaining the origin of the asymmetrical lateral lobes of the fusca-rugosa series of Phyllophaga.

The strongly developed basal piece is surmounted by a simple, symmetrical pair of lateral lobes, which are continuous above, and united below by a frail chitinous arch or bridge. The median lobe, when extended through the opening between the lateral lobes of this simple tegmen, has almost exactly the appearance of a second smaller tegmen.

This tegmen-like median lobe is characteristic, in that it consists of a simple partial tube, uniformly chitinous above and membraneous beneath, similar in these relations to

the typical basal piece in Phyllophaga; and surmounting this tubular portion is a strongly asymmetrical chitinous structure, articulated with it in much the same manner as the united lateral lobes are articulated with the basal piece of the tegmen. The median orifice in this form of medial lobe is the opening through the arch or collar-like, asymmetrical, chitinous, apical portion described above.

The species from Trinidad was represented by two specimens, a male and a female. The genital tube of the male had been removed, and as is too often the case, the median lobe had been broken off and thrown away; so the observations noted above could not be verified from this specimen. These two forms - from St. Vincent Island and from Trinidad, respectively - are structurally very similar, however, and the median lobes of the male genital tubes would certainly be of the same type.

Another significant fact is that both of these forms have one of the male hind tibial spurs fixed, and they also have ten jointed antennae; both of which are characters found nowhere else in the West Indian material studied. These forms, however, belong distinctly to the South American and not to the West Indian fauna.

A striking, but probably not an especially significant fact, is the general agreement between the superficial characters with those leading to the fusca-rugosa series, in Horn's key to the species of temperate North America. If these two forms were placed unlabeled in a collection of North American Phyllophaga by the key characters they would go directly into that group, and only the absence of the characteristic sculptur-

ing of the under side of the male abdomen would indicate the error.

## THE CONGRUA DISPAR SERIES

The congrua-dispar series is distinctly southeastern in its distribution, being limited, except for a few species, to the same range as that of the typical coastal plains fauna. This series, in common with the two remaining series, has the lateral lobes of the male genital tube symmetrical, and without a basal collar-like portion. In continental North America it is typically separated from the next two groups by the fixed male hind tibial spur, which however, may be very short or even absent.

While this series, of which congrua, hirtiventris, dispar, and ephilida are representative species, is typically continental in thefact that all but one of the forms assigned to it have a fixed male hind tibial spur, (a character which does not occur in the related Antillean forms studied) it is still so closely allied to the Antillean fauna that in a few instances, as in the dispar group, the male genital pattern is very close to that of certain Cuban forms - so close, indeed, that certain Cuban species and the corresponding continental forms would unhesitatingly be grouped together.

Although the relation of this series to the Antillean section of the genus is so strongly marked, the time elapsing since it became established on the continent is sufficient to afford ample opportunity for marked independent differentiation on the mainland. For example, the congrua type of male genital characters finds apparently the nearest related type in Porto Rico, while on the mainland, this type is represented by at

least four distinct forms.

## THE CRENULATA SERIES

The crenulata series of Phyllophaga is typically southwestern, and reaches its highest development in the southwestern United States and in Mexico. This series in temperate North America is characterized by a very simple type of male genital tube, in which the median lobe is very much reduced, or absent, and the lateral lobes are of the simplest type found in the genus. This series is typically represented by the species crenulata, fucata, exorata, etc. In this series, as also in the next, both of the male hind tibial spurs are always free.

Outside of the region typically occupied by it, this series is represented in the United States only by a few forms, which are confined to the extreme southern, or to the semi-arid portions, except the cosmopolitan species crenulata, which has the extratypical range indicated on the accompanying map. The distribution of this series in the tropical portion of its range has not yet been studied with any degree of exactness; but apparently it ranges south, as far as northern South America.

The crenulata series is related to certain elements of the Antillean Phyllophaga, but it evidently does not trace its connection with that section of the genus, through

temperate North America, and its affinities in that direction can probably be well understood, only after it has been more thoroughly studied in tropical America.

## THE TRISTIS SERIES

The male genital structures in this series are characteristic, and conform closely to one type, so that its relationships are not clearly evident. There is some structural evidence, however, of a relationship, on the one hand, with certain groups assigned to the crenulata series, and on the other hand, with some of the more generalized forms in the congrua-dispar series; but no form that is directly, or even definitely allied to the tristis series has studies from the West Indes.

The tristis series apparently belongs to tropical North America more distinctly than any of the other three series discussed, for it is represented in temperate North America by only five species in all, while it contains many Mexican and Central American forms that do not extend their range north of Mexico. Outside of Texas, New Mexico, and Arizona, it is represented in temperate North America only by the single species tristis Fabr., while to the south its range extends well into South America.

It is typically represented by the species tristis, crinita, and antennata, all of which occur in the region studied.

## ORIGIN OF THE PRESENT RELATIONS OF PHYLLOPHAGA IN TEMPERATE NORTH AMERICA

The present association of the four series of Phyllophaga in temperate North America has evidently developed as a result of invasion from two directions - from the southeast, and from the southwest. The two series that are characteristically southwestern have been derived directly from their more southern centers of differentiation. They consist chiefly of the more widely distributed or"pioneer" members of their respective groups, and they must be recognized as such, in their relation to these studies. The two series that are typically eastern, however, present each a distinct problem of its own. The congrua-dispar series is closely allied to the Antillean section of Phyllophaga, and its continental center of differentiation and dispersal lies in the extreme southeastern part of the United States. In its distribution it belongs typically to the coastal plain fauna, (See Plate XXVI). The fusca-rugosa series, on the other hand, is sharply separated from all of the associated series by the characters of the male genital tube, and its nearest relatives seem to occur in South America. It certainly is not derived from any nearer source. Its center of differentiation and dispersal, lies in the southern Applachian region, and its range is more characteristically north and west from this center than it is toward the south. It never occurs in the tropics.

The most plausible hypothesis for explaining the present relations of the fusca-rugosa series and the congrua-dispar series of Phyllophaga, is that they entered temperate North America from the southeast, by way of the West Indies, over land connections that have probably existed in past Geological ages between the southeastern United States, and South America or Central America.

Studies both of geographic distribution and of dynamic geology furnish evidence which seems to show that such land connections have existed. Simpson says: "There appears to be good evidence of a general elevation of the Greater Antillean region, probably some time during the Eocene, after most of the more important groups of snails had come into existence, at which time the larger islands were united, and there was land connection with Central America by way of Jamaica and possibly across the Yucatan Channel, and there was then a considerable exchange of species between the two regions. At some time during this elevation there was probably a landway from Cuba across the Bahaman plateau to the Floridian area, over which certain groups of Antillean molluscs crossed". (Simpson, Charles Torrey, Distribution of Land and Fresh Water Molluscs of the West Indian Region, and their Evidence with Regard to Past Changes of Land and Sea, Proc. U. S. Nat. Mus., Vol. XVII, p. 447, 1894).

Spencer, (Reconstruction of the Antillean Continent, Bull. Geol. Soc. Am., Vol. 6, 1895) recognizes three periods of elevation of the Antillean region, occurring in the Eocene, Pliocene, and early Pleistocene periods, during each of which, North and South America were united by a land bridge. Three periods of elevation alternated with periods of subsidence, during some of which, the Antilles were reto a few small islands.

The stupendous oscillations described by Spencer are wholly unnecessary to account for the present relations of the series of Phyllophaga in eastern North America. Even a continuous land connection at any one time is not required. It is enough to suppose that at some time, South American Phyllophaga were able to reach the hypothetical Antillean continent over a land bridge, either directly or by way of Yucatan, and that, later, they were able to reach the Floridian region over a similar land connection. Here, they became isolated by the subsidence of the land bridge that they had last crossed. Continued subsidence forced them out of the coastal plains region into the Southern Appalachian highlands, where the evolution of the fusca-rugosa series began.

The corresponding subsidence of the Antillean region reduced this land mass to a few small islands, when the

resulting environmental stresses caused the extermination of many forms, and profound modifications in the survivors. It was these modified Phyllophaga which came later to stock the reelevated Antillean lands, and during the Pleistocene period, to migrate to the main continent over another temporary land bridge, the subsidence of which isolated the ancestors of the congrua-dispar series.

## EXPLANATION OF TERMS

The following list of the terms used by Sharp and Muir in their work on the "Comparative Anatomy of the Male Genital Tube in Coleoptera", and adopted in this paper ~~per~~ for the corresponding structures in Phyllophaga, has been taken bodily from the work of these authors (Trans. Ent. Soc. Lond. 1912, part 3, pp. 481-483).

Aedeagus. The median lobe and tegmen together. It is the Edeagophore of Blaisdell.

Azygos, or the azygotic portion of the male genital tube. It comprises all the unpaired portion of the tube from the body wall to the divergence of the seminal ducts, where the zygotic portion, or efferent ducts, ends (b-d and 5-1, pl. 1).

Basal-piece (bp). The basal part of the tegmen. It is the "basale" (Blaisdell); external lobes (Packard); basalplatte (Verhoeff); tambour (Straus-Durckheim).

Ejaculatory duct (ej) or stenazygos is the slender portion of the genital tube from the seminal ducts to the interior sac or eurazygos.

Eurazygos (c-d and 5-1, pl. 1). The enlarges portion of the genital tube.

First connecting membrane (cm1). The membrane connecting the median lobe to the tegmen.

Internal sac (is) The enlarged portion of the azygos which is more or less evaginated during copulation. It is the sac interne (Jeannel); praeputialsack (Verhoeff), and forms part of the ejaculatory duct of most writers.

Lateral lobes (ll). The distal portion of the tegmen. In the generalized trilobe type they form two free processes lateral of the median lobe and and often enveloping it. They are the "deux branches de la pince" (Straus-Durckheim); mesostili in Procrustes, ipofallo in Lucanus and perifallo in Dytiscus (Berlese); apicale (Blaisdell), lateral lobes (Packard), Parameren (Verhoeff).

Median foramen (mf). The aperture, or lumen, at the base of the median lobe through which the ejaculatory duct passes.

Median lobe (ml). The central portion of the aedeagus upon which the median orifice is situate. It is the penis of Straus- Durckheim, Verhoeff, Packard and many other writers, Körper (Lindemann), body (Hopkins), ipofallo in Procrustes etc., and penis in Oryctes (Berlese).

Median orifice (mo). The opening, or area, on the median lobe through which the internal sac is evaginated. It is the "Mundung ductus ejaculatorius" (Verhoeff), fornix edeagi (Blaisdell) and apical opening (Hopkins).

Median strut (ms). A single strut, or pair of struts, proceeding from the basal part of the median lobe. In some cases they are articulated to the median lobe, in

other cases they actually form part of the median lobe without articulation or line of demarkation.

Point of articulation (pa). The point on the median lobe to which the lateral lobes are attached. In many cases the median lobe and tegmen are connected by intervening membrane and there is no point of articulation.

Second connecting membrane (cm2). The membrane connecting the tegmen to the termination of the abdomen. It is the prepuce of Straus-Durckheim (Melolontha vulgaris).

Spicule (sp fig. 224a). A sclerite attached by one end to the second connecting membrane. In many cases it is Y- or T- shaped. It is the Stengel (Lindemann), spiculum gastrale (Verhoeff), rod or fork (Hopkins), and is considered by some as being the last sternite. It is not infrequently similar in shape to another sclerite that pertains to another layer of the genital tube.

Stenazygos. Is the stenazygotic or slender portion of the azygos (b-c, pl. 1).

Tegmen (tg). The term applied to the lateral lobes and basal-piece together. It is the ring (Hopkins), Gabel (Lindemann).

Ventral plate. A sclerite on the anterior ventral surface of the basal-piece of some Lamellicorns. In some cases

the lateral lobes are consolidated to its anterior edge. The chitinization of this part varies much.

Zygos. Zygotic portion of the male genital tube; and is formed by the two seminal ducts (a-b, pl. 1) proceeding from the testes.

## BIOGRAPHICAL

Robert Douglas Glasgow received the degree of Bachelor of Arts in Entomology from the University of Illinois in 1908. He received a scholarship in entomology in the Graduate School of the University of Illinois for the year 1908-1909, was assistant in entomology during the years 1909-1911, a fellow in entomology during the year 1911-1912, and student assistant in the Office of the State Entomologist during the year 1912-1913.

He is a member of Sigma Xi, Illinois Chapter; of the American Association for the Advancement of Science; of the Illinois Academy of Science; and the Entomological Society of America.

PLATE I

PLATE I

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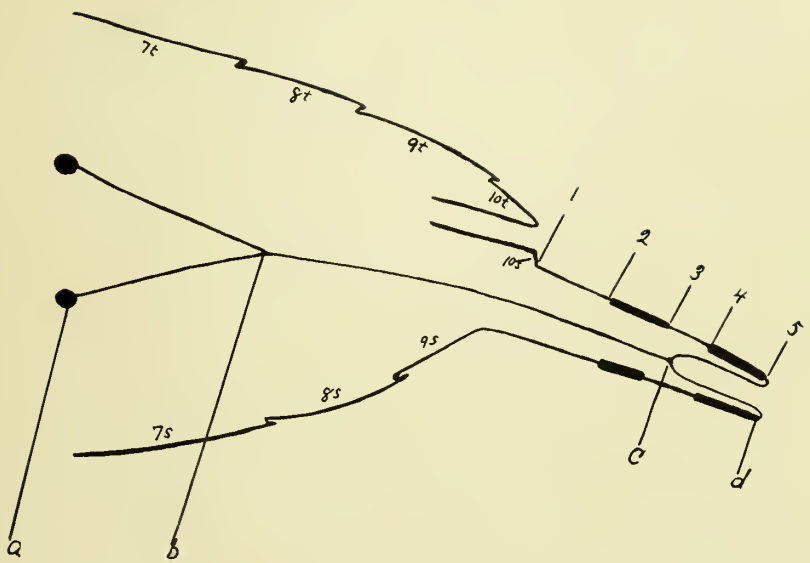
Diagrammatic figure, showing relations of the various parts of the male genital tube in Coleoptera

From Sharp and Muir.




Diagrammatic figure showing general relations of the parts of the typical male genital tube

From Sharp and Muir

PLATE II

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*Phyllophaga hirticula* Knoch.

Male genital structures

Type specimen

Eastern form

PHYLLOPHAGA HIRTICULA Knoch

Type Specimens

♂ & ♀ Genital Structures

PLATE III

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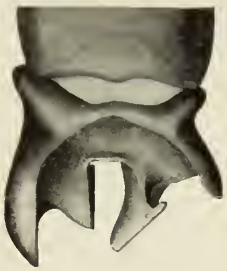
*Phyllophaga hirticula* Knoch.

Western form

# LACHNOSTERNA HIRTICULA KNOCH.

## Male Organs.



4. Dorsal aspect.

3. Lateral aspect, Left.

1. Caudal aspect.

2. Lateral aspect, Right.

5. Ventral aspect.

## Female Organs.

8. Lateral aspect, Left.

6. Caudo-ventral aspect.

7. Lateral aspect, Right.

PLATE IV

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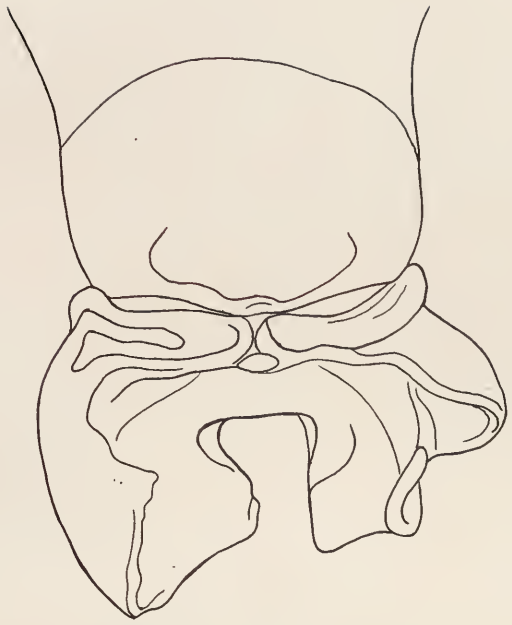
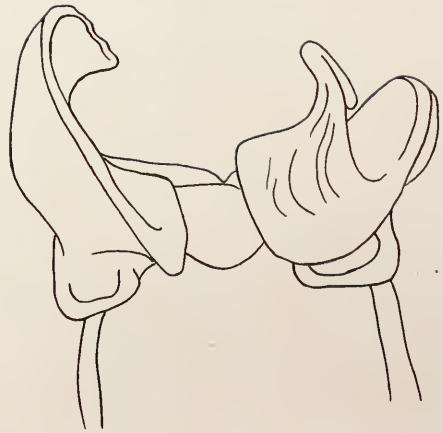
*Phyllophaga hornii* Smith

Male genital structures

Type specimen





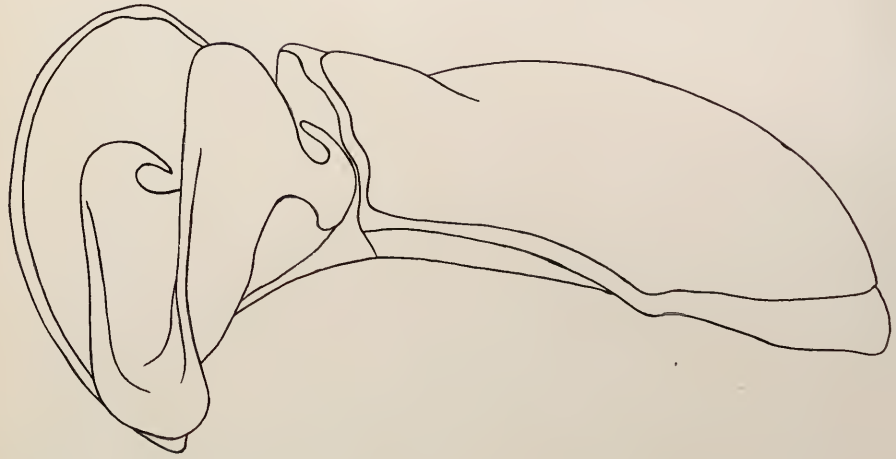


PLATE V

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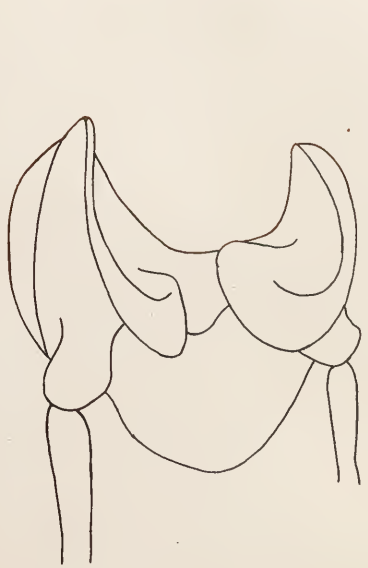
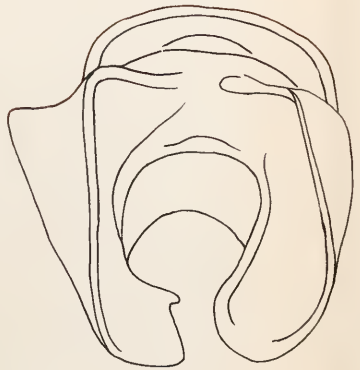
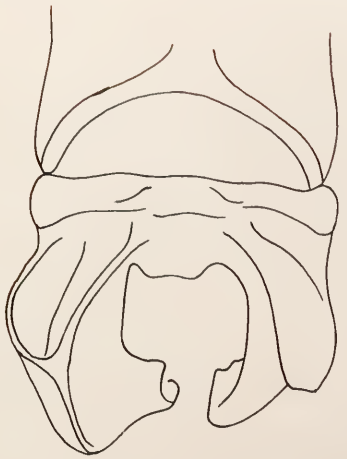
*Phyllophaga profunda* Blanchard

Male genital structures

From type of P. biimpressa Smith







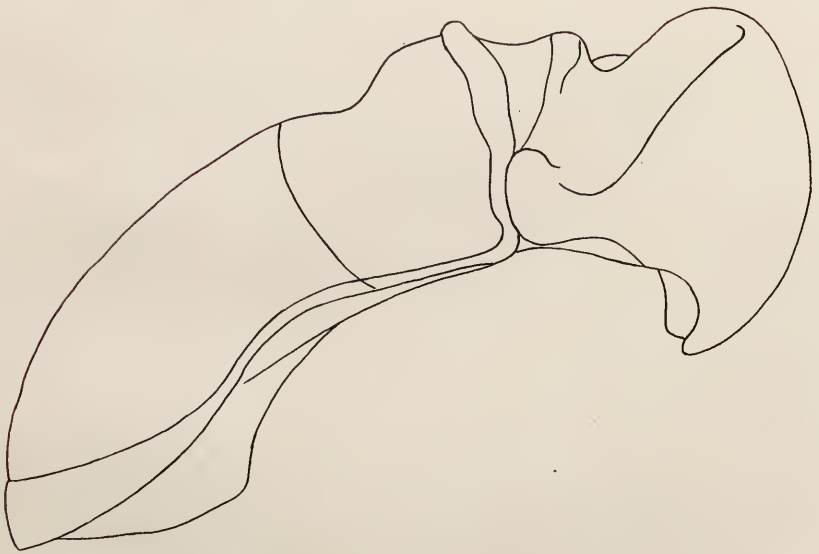


PLATE VI

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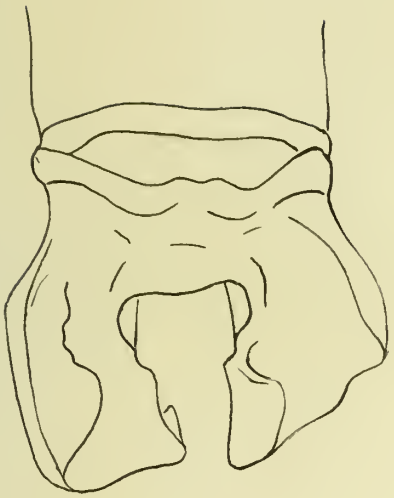
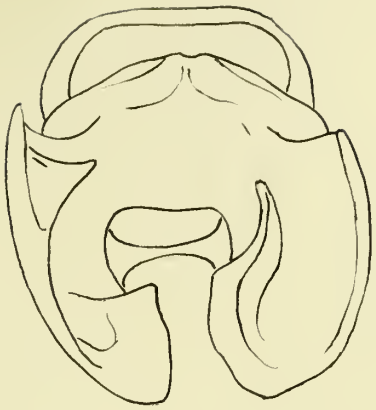
Phyllophaga rugosa Melsheimer

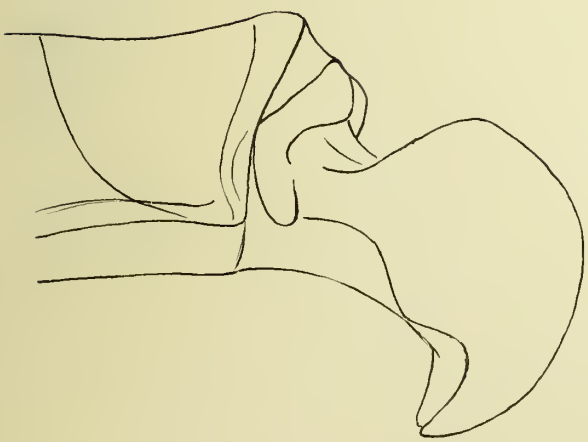
Male genital structures

Type lost

From form designated by LeConte and by Horn







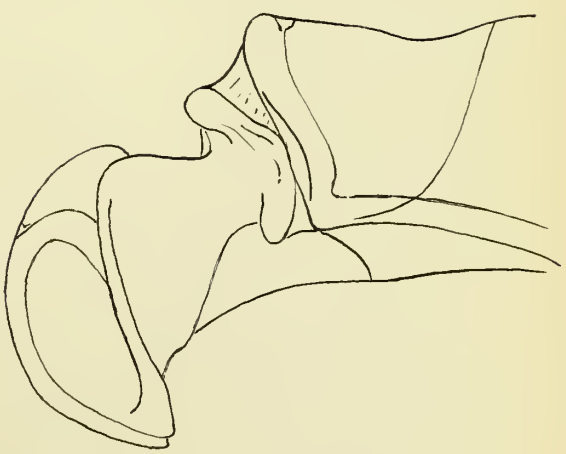


PLATE VII

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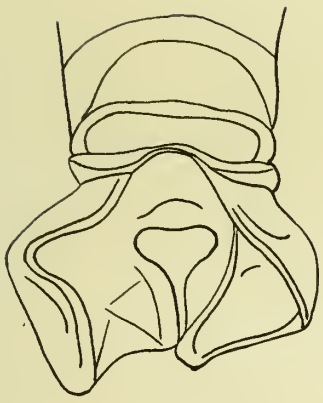
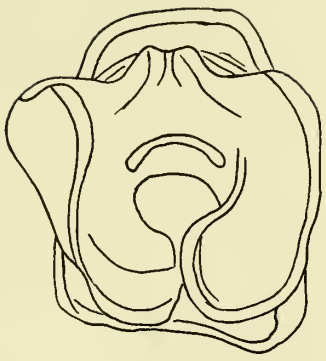
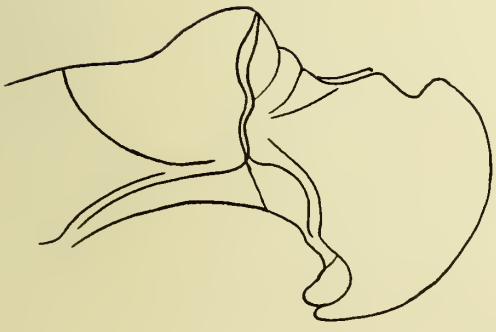
*Phyllophaga fraterna* Harris

Male genital structures

Compared with type specimen







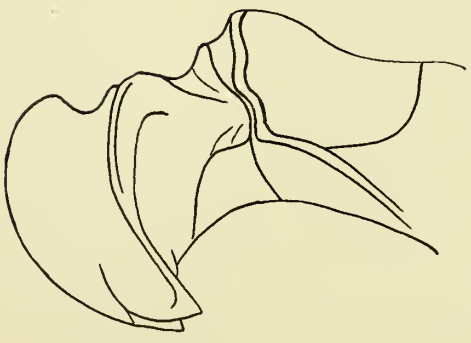


PLATE VIII

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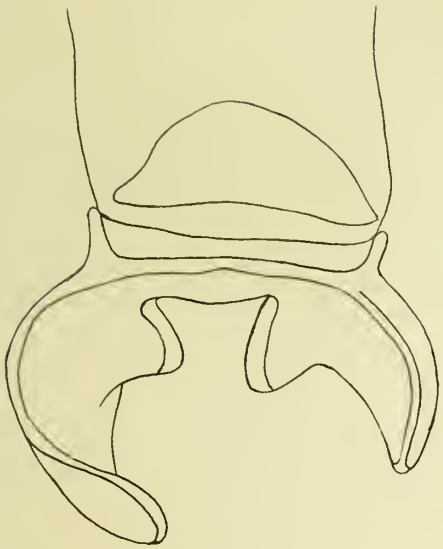
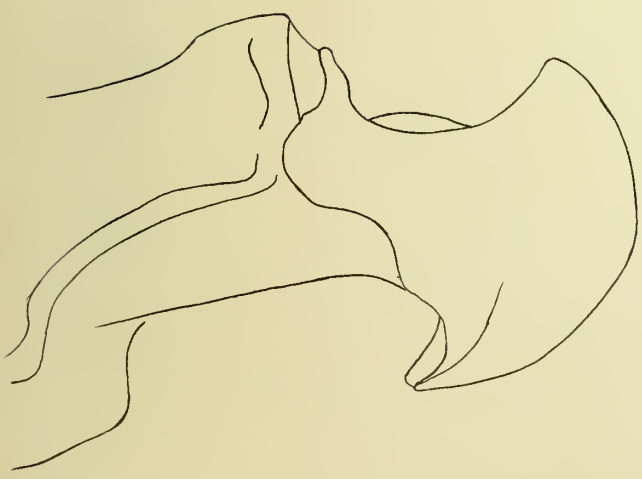
*Phyllophaga delata* Horn

Male genital structures

Type specimen





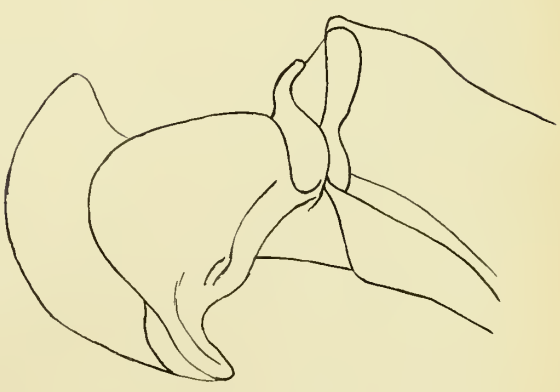


PLATE IX

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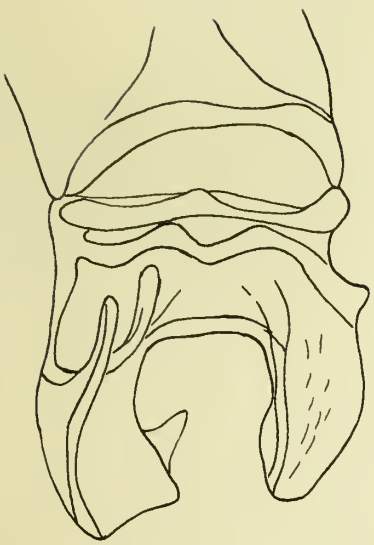
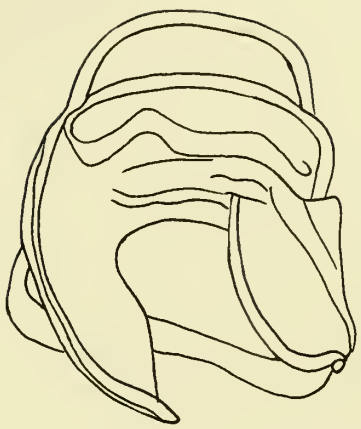
*Phyllophaga infidelis* Horn

Male genital structures

Type specimen





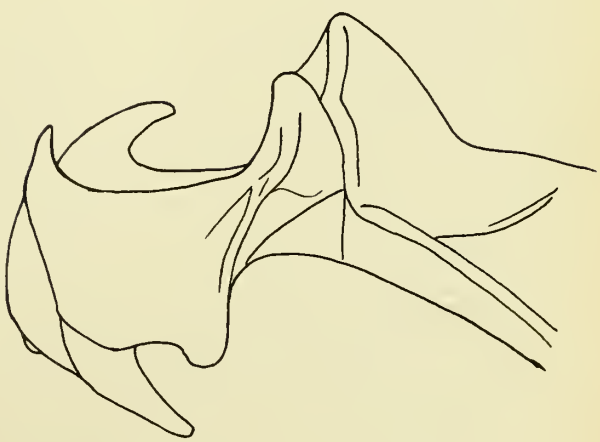


PLATE X

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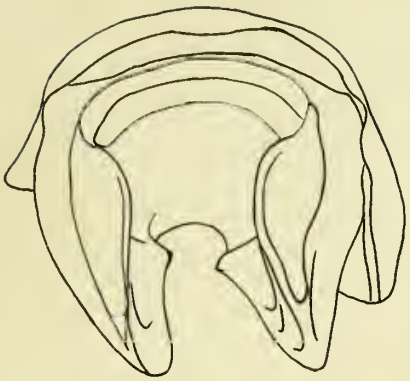
*Phyllophaga drakii* Kirby

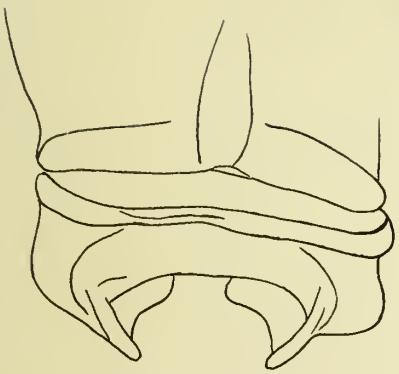
Male genital structures

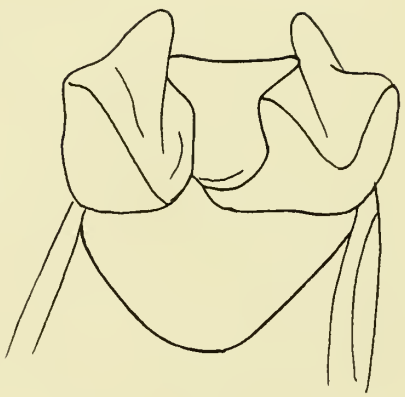
From type of *dubia* Smith

Compared with drawings of type specimen

of *drakii*







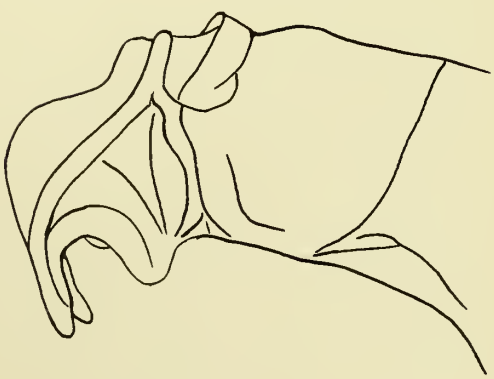


PLATE XI

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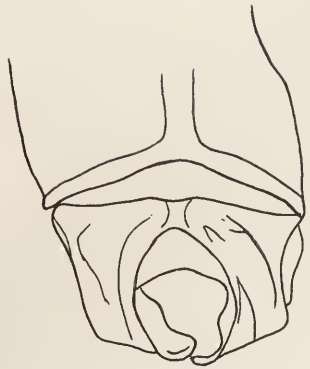
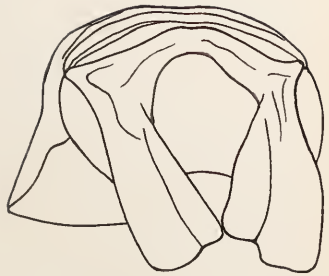
Phyllophaga fervida Fabricius

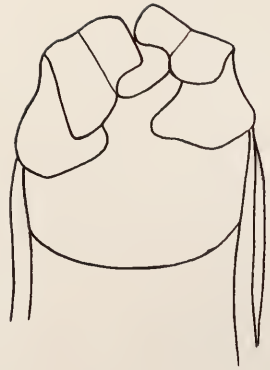
Male genital structures

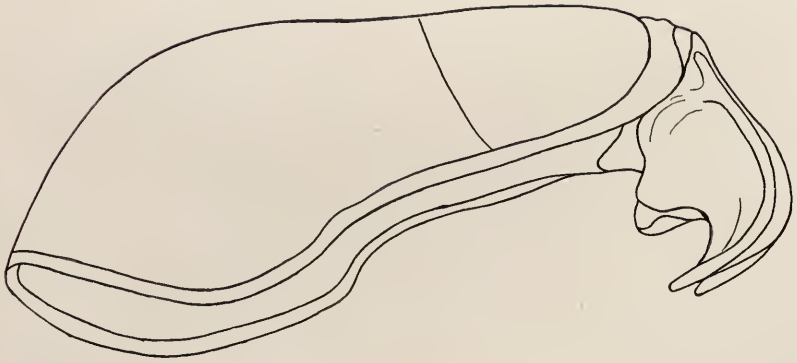
From type of arcuata Smith

Compared with drawings of type of fervida Fabr.









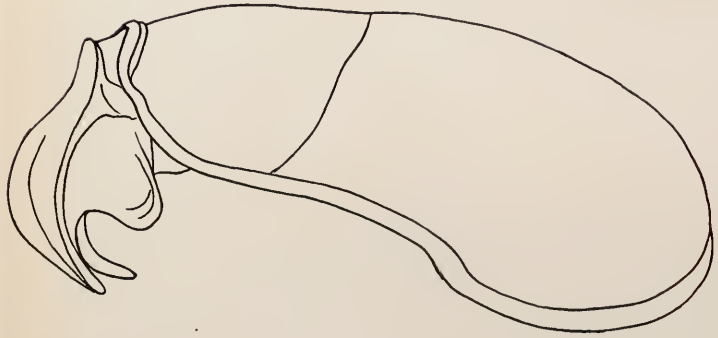


PLATE XII

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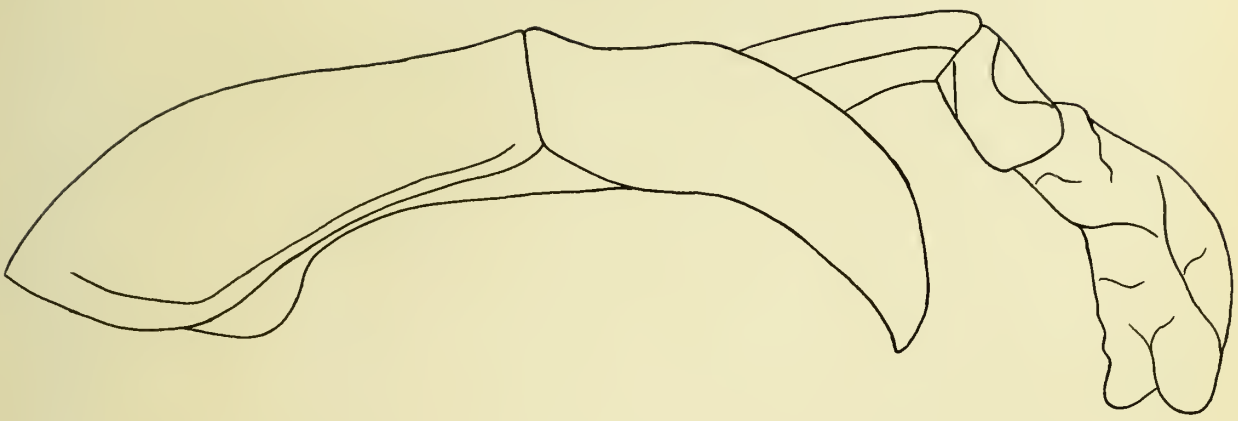
Phyllophaga sp.

Form from St. Vincent Island, representing probable nearest relatives of the Fusca-Rugosa series

Showing median lobe resembling a small second tegmen, with asymmetrical apical piece resembling a second pair of lateral lobes

Irregular mass at extreme apex is the dried everted internal sac



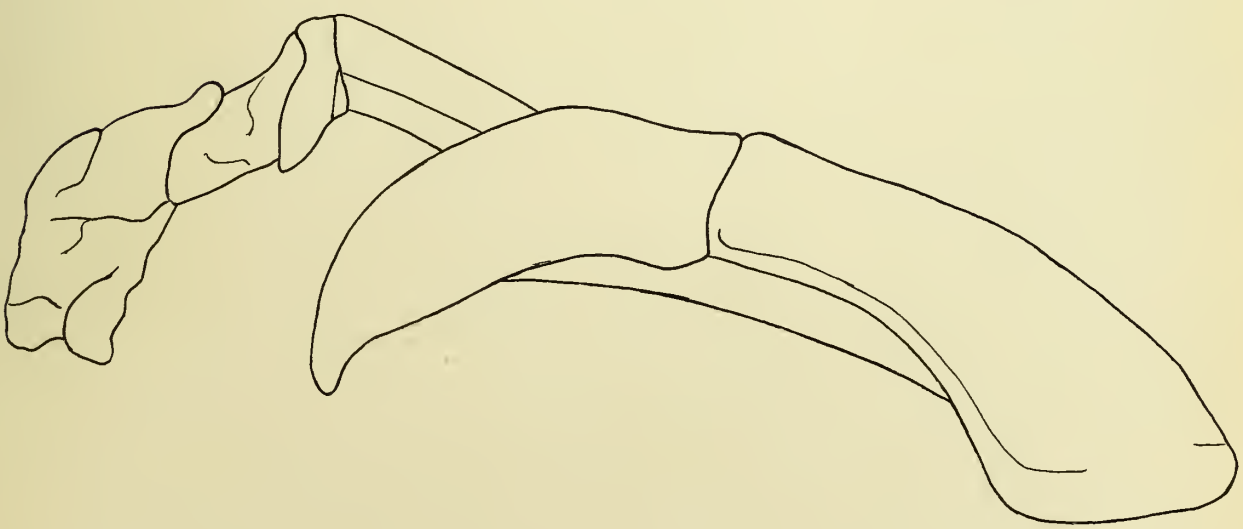


PLATE XIII

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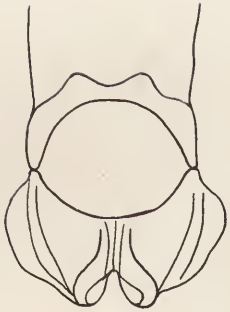
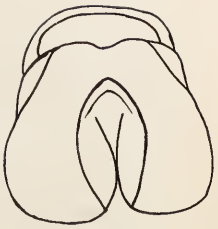
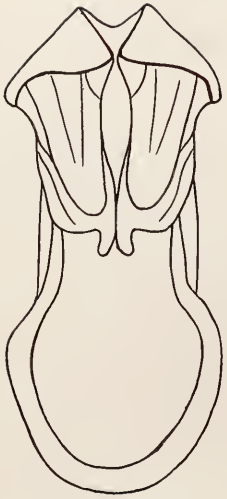
*Phyllophaga hirtiventris* Horn

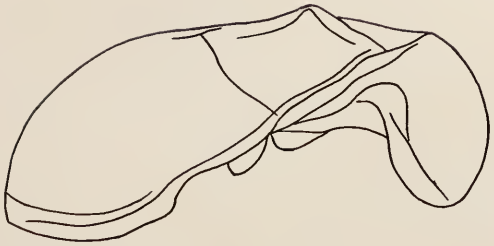
Male genital structures

Type specimen









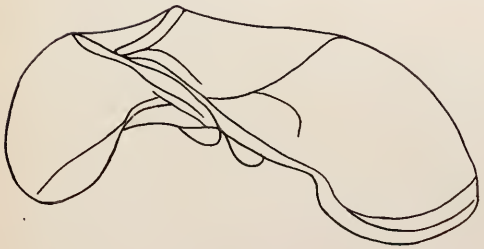


PLATE XIV

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*Phyllophaga parva* Linell

Male genital structures

Type specimen

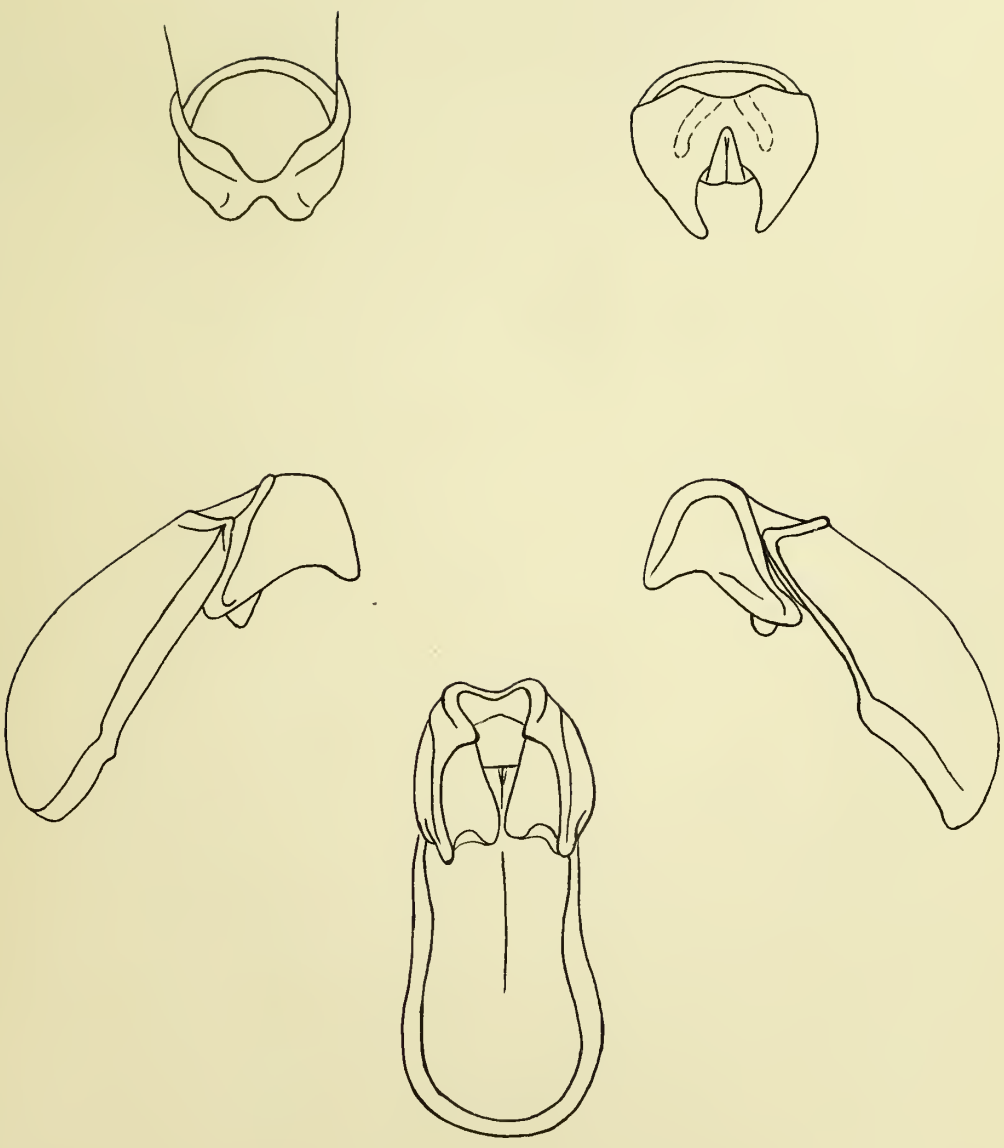

PLATE XV

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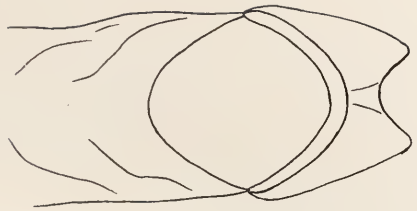
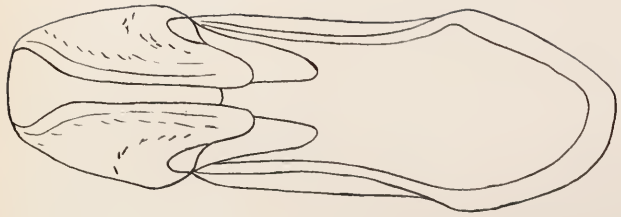
*Phyllophaga clypeata* Horn

Male genital structures

Type specimen





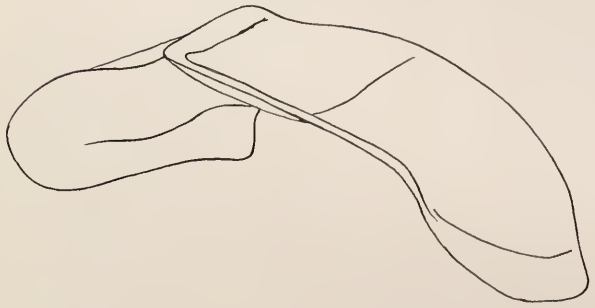


PLATE XVI

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*Phyllophaga fucata* Horn

Male genital structures

Type specimen

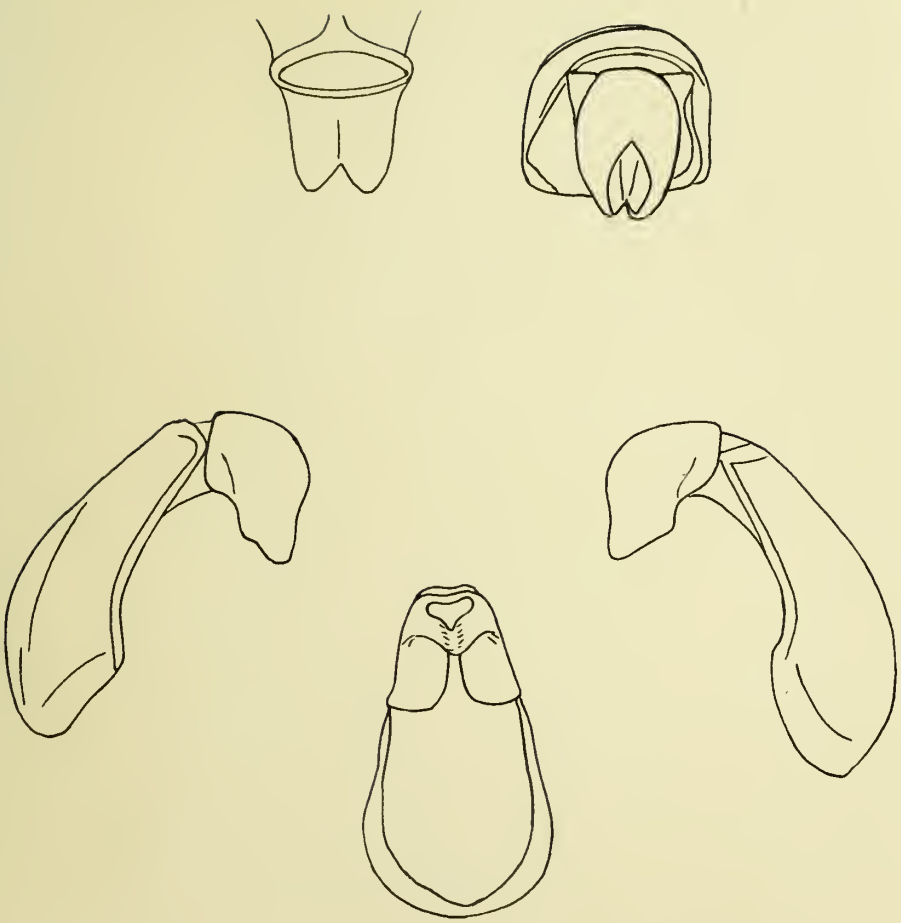

PLATE XVII

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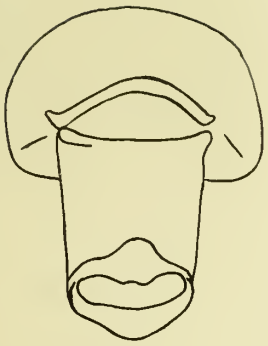
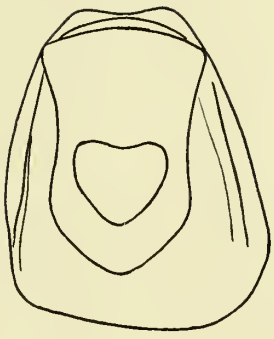
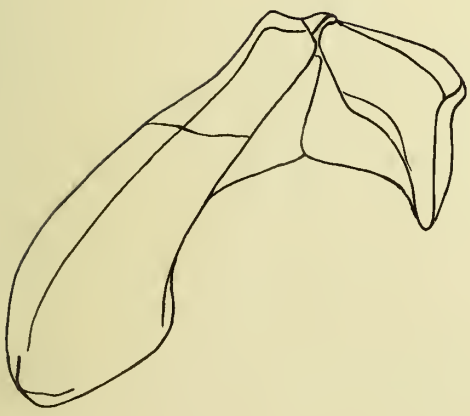
*Phyllophaga exorata* Horn

Male genital structures

Type specimen







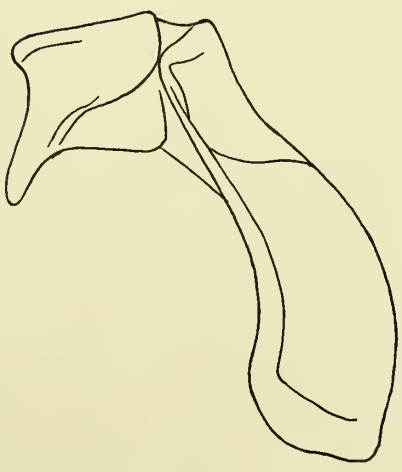


PLATE XVIII

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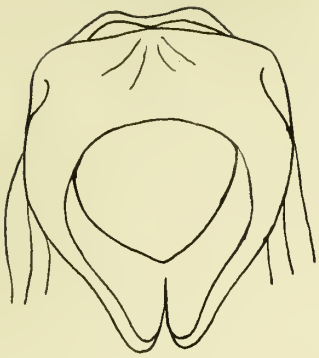
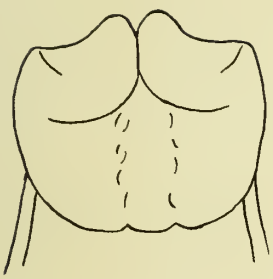
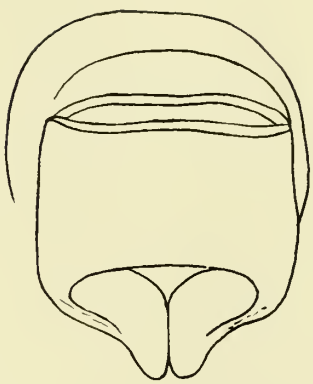
Phyllophaga aemula Horn

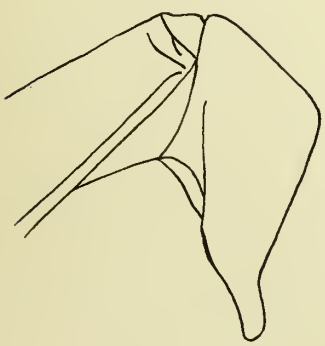
Male genital structures

Type specimen









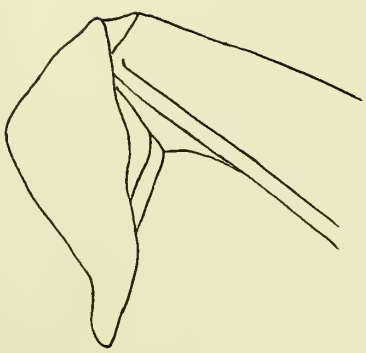


PLATE XIX

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*Phyllophaga inepta* Horn

Male genital structures

Type specimen

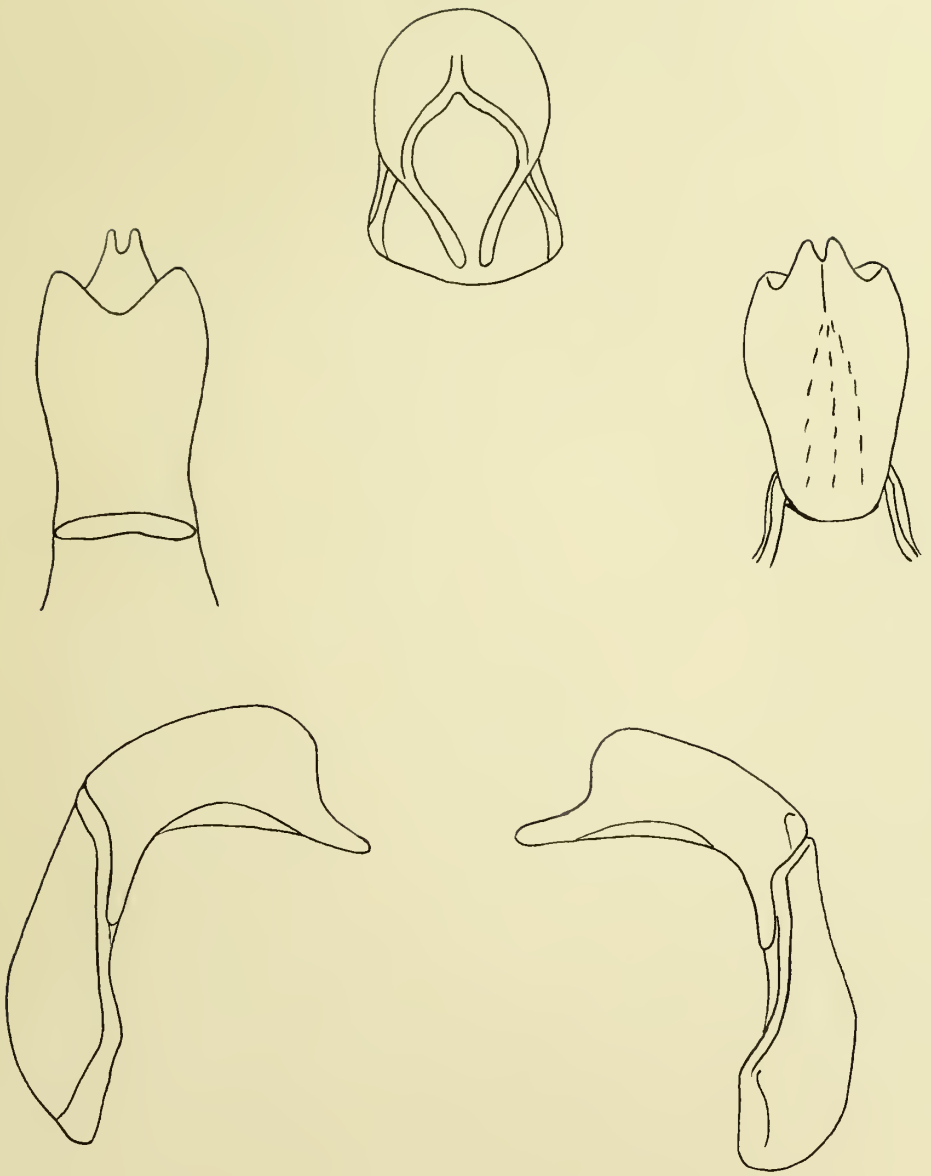

PLATE XX

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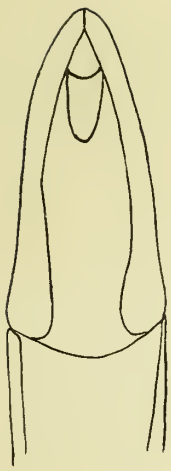
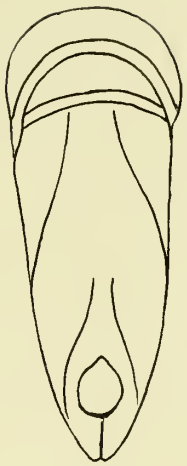
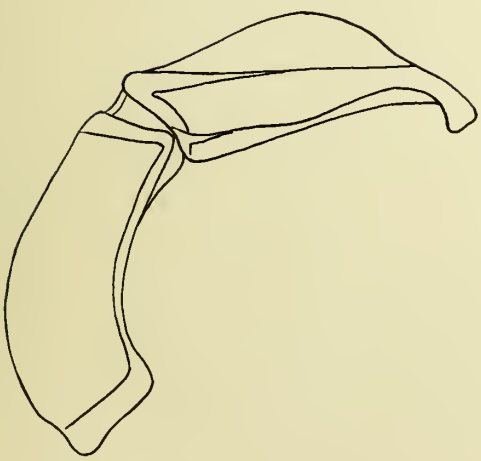
*Phyllophaga ignava* Horn

Male genital structures

Type specimen







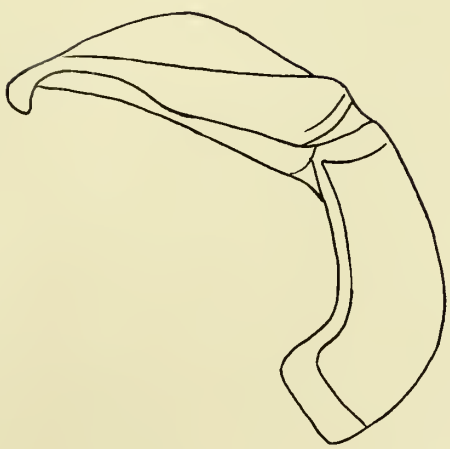


PLATE XXI

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*Phyllophaga antennata* Smith

Male genital structures

Type specimen

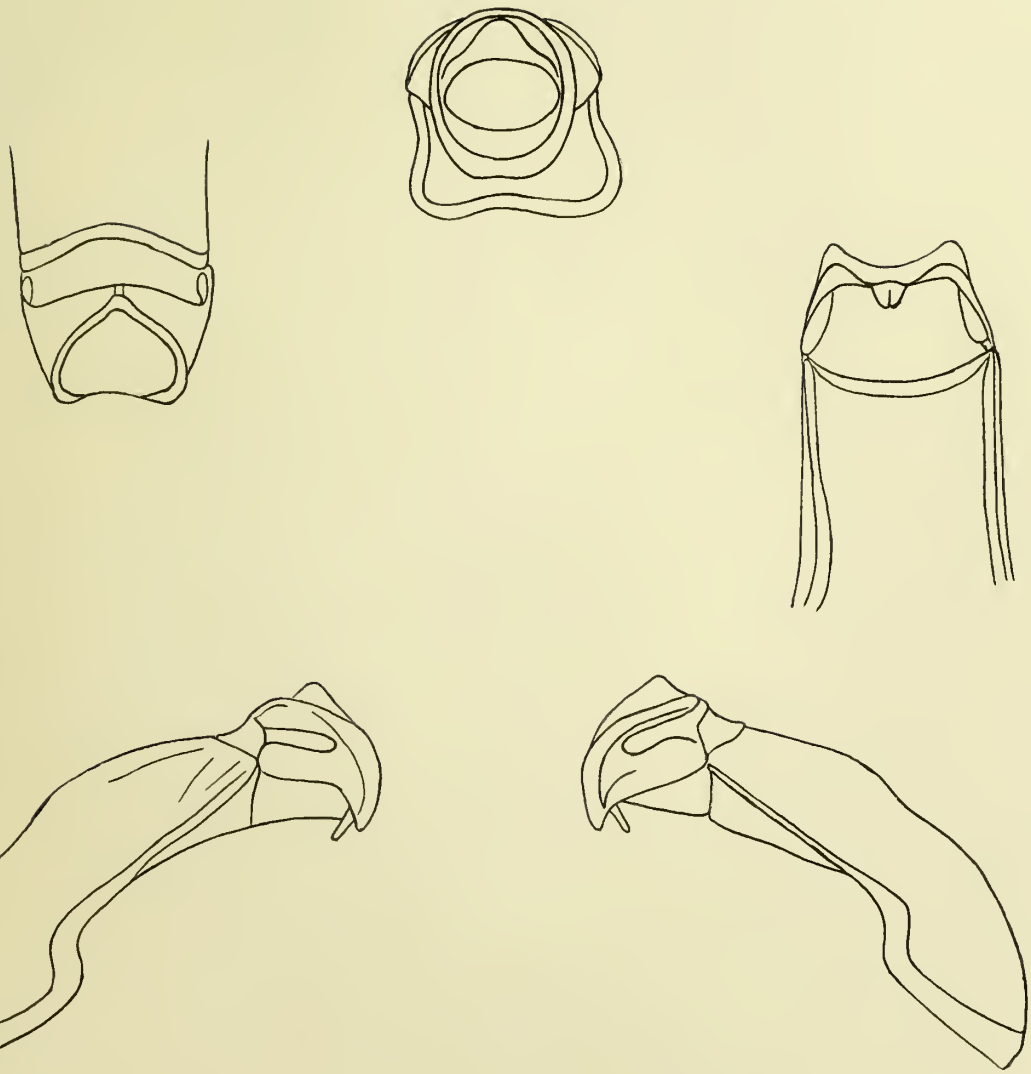

PLATE XXII

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*Phyllophaga crenulata* Fabricius

Male with tegmen extruded, and with internal sac everted, showing absence of median lobe

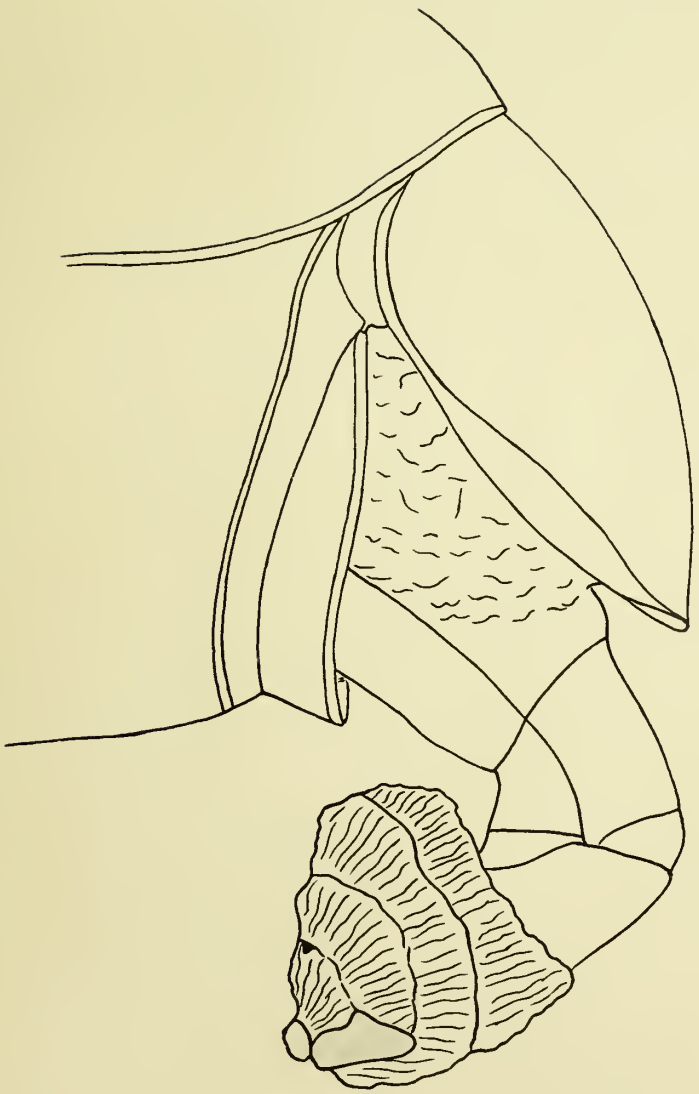

PLATE XXIII

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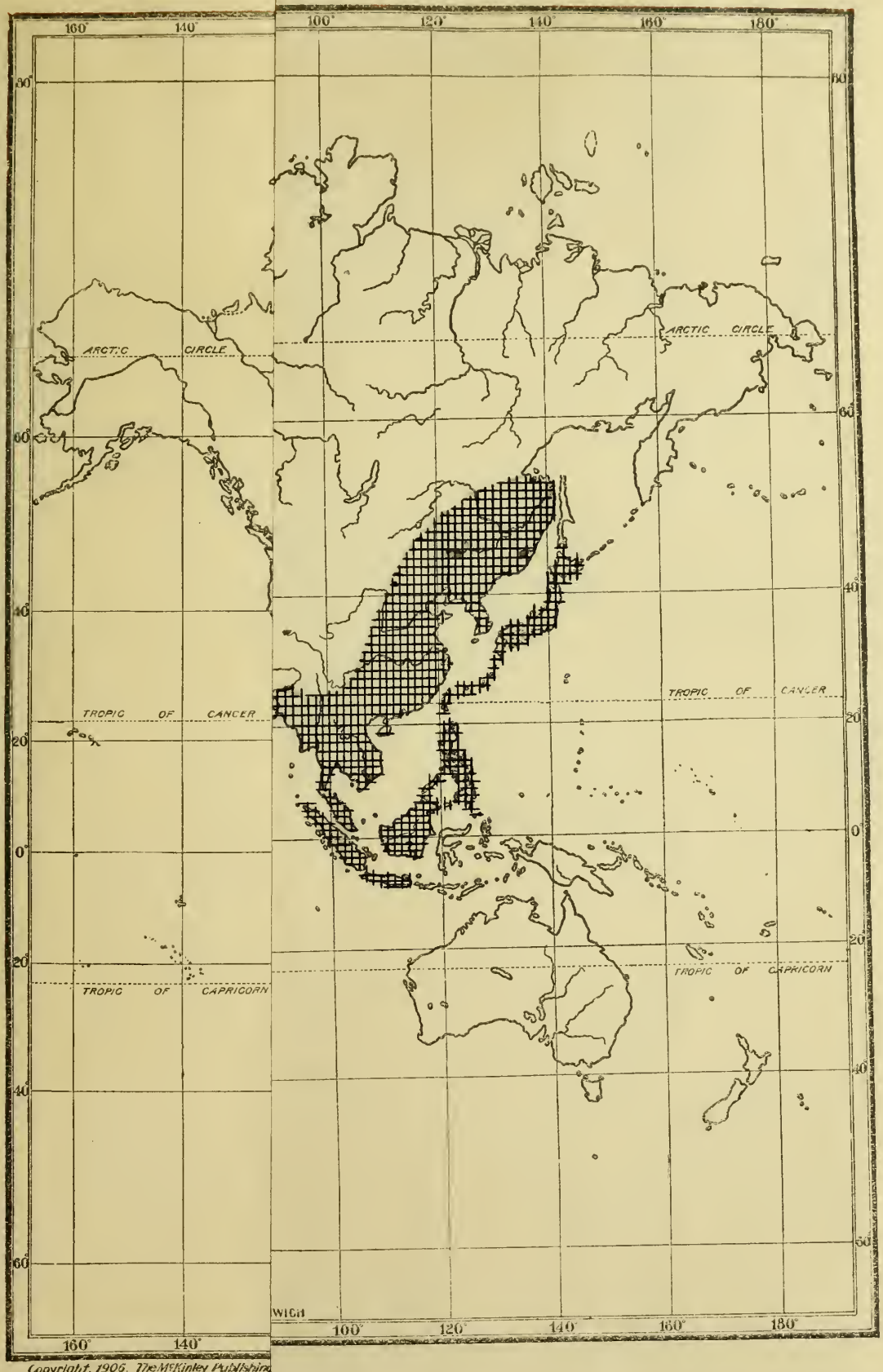
Extreme range of the genus *Phyllophaga*

CATOR'S PROJECTION).



McKINLEY'S DESK OUTLINE MAPS. DOUBLE SIZE. No. 201 **THE WORLD** (MERCATOR'S PROJECTION).

PLATE XXIV

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Range of the *Fusca*-*Rugosa* series of *Phyllophaga*

Cross Hatching = typical range of the series

Horizontal Ruling = extreme range

GOODE'S SERIES OF BASE MAPS. No. 2. NORTH AMERICA

PLATE XXV

---

Range of the Fusca-Rugosa series of Phyllophaga, and location of nearest known relatives

Cross Hatching = typical range

Horizontal Ruling = extreme range in temperate North America

Vertical Ruling = territory occupied by nearest known relatives

PROJECTION).

McKINLEY'S DESK OUTLINE MAPS. DOUBLE SIZE. No. 201 **THE WORLD** (MERCATOR'S PROJECTION).

PLATE XXVI

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Range of the Congrua-Dispar series

of Phyllophaga

Cross Hatching = typical range

Horizontal Ruling = extreme range in temperate North America

Vertical Ruling = territory occupied by most nearly related forms

GOODE'S SERIES OF BASE MAPS. No. 2. NORTH AMERICA

PLATE XXVII

---

Range of the Crenulata series

of Phyllophaga

Cross Hatching = typical range

Horizontal Ruling = extreme range in temperate North America

Vertical Ruling = territory occupied by related forms

GOODE'S SERIES OF BASE MAPS. No. 2. NORTH AMERICA

PLATE XXVIII

---

Range of the Tristis series of

Phyllophaga

Cross Hatching = typical range

Horizontal Ruling = extreme range

GOODE'S SERIES OF BASE MAPS. No. 2. NORTH AMERICA